A LATE SILURIAN FLORA FROM THE LOWER OLD RED SANDSTONE OF SOUTH-WEST DYFED

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ABSTRACT. This extensive compression flora from the late Silurian (Downtonian) of South Wales contributes to our understanding of terrestrial vegetation relatively early in the colonization of the land by predominantly vascular plants. The large number of fertile *Cooksonia* specimens has resulted in an amplified diagnosis of *C. hemisphaerica* Lang for which intraspecific variation is demonstrated; in the erection of a new species, *C. cambrensis*, and in records of plants close to *C. caledonica* and *C. pertonii*. Elongate sporangia on unbranched twisted stalks are named *Tortilicaulis transwalliensis* gen. et sp. nov. and affinities with bryophytes and vascular plants are discussed. *Hostinella* is the commonest stem type, but some smooth axes show departures from dichotomous branching. In addition, axes with triangular and truncated spines are described indicating, together with the above, a diversity of taxa and morphological organization. A short progress report on our studies of the early history of vascular plants in the South Wales area is presented.

W. H. LANG's classic paper on the Downtonian (approximately equal to Pridoli) floras of southern Britain was published over forty years ago (1937), but the fundamental importance of his meticulous work has been fully appreciated only recently in the upsurge of interest in the early evolution of land plants (for example, Banks 1975*a*, *b*). His genus *Cooksonia* is now recognized as one of the most completely known early vascular plants (see Addendum in Gray and Boucot 1977), although axes with convincing tracheids have never been found attached to sporangia. *Cooksonia* has since been recorded from Downtonian localities in Czechoslovakia (Obrhel 1962), Libya (Daber 1971), U.S.A. (Banks 1973), and Podolia (Ishchenko 1975), and from younger strata in Scotland (Edwards 1970), Wales (Croft and Lang 1942), and the U.S.S.R. (Ananiev and Stepanov 1969; Yurina 1969). It is from these Devonian horizons that new species have been described, workers on Downtonian floras either having been reluctant to identify often very fragmentary and relatively featureless fossils to a specific level, or having assigned them to one of Lang's original species, *C. pertonii* or *C. hemisphaerica*.

Indeed apart from Lang's work, little is known about land vegetation in the late Silurian: vascular plant remains usually comprise sterile, rather featureless axes (for example, Høeg 1942) often associated with the highly problematical non-vascular genera *Prototaxites* Dawson and *Pachytheca* Hooker. An exception is the Podolian flora (Ishchenko 1969, 1975) which contains numerous, but unfortunately poorly illustrated plants, many of which are of uncertain affinity. The flora at Freshwater East, Dyfed is also an extensive one. It was first recorded by Dixon in 1921, and Lang himself illustrated a few specimens in his 1937 paper. My own collection, amassed over several years and now housed at the National Museum of Wales, contains

abundant plant remains including sterile and fertile axes of rhyniophyte type as well as *Nematothallus* Lang, *Prototaxites* and *Pachytheca*. The fossils are very fragmentary, indeed of the kind commonly cited in geological literature as 'plant debris', but it is important that any plants of this age be carefully and critically described prior to any speculation on the early history of land vegetation. In this study, the variety of form in the sterile axes indicates a diversity of taxa hitherto unknown in British Downtonian floras, while the occurrence of a large number of *Cooksonia* sporangia permits, for the first time, a study of inter- and intraspecific variation in the genus.

OCCURRENCE AND PRESERVATION

Patches of drifted plant and animal fragments occur throughout a layer of grey-green micaceous sandstone some 0·3 m thick within a typical O.R.S. red-bed sequence on the north side of Freshwater East Bay (Nat. Grid Ref. SS09 0236 9812). Dixon (1921) had placed these plant-bearing horizons at the top of his Basement Beds of the O.R.S., which he regarded as the *Thyestes* (*Auchenaspis*) stage of the Downtonian, a conclusion supported by King (1933) who equated the beds to the Ledbury marls and sandstones (1.2) of the Welsh Borderland. Further support for a Downtonian age comes from the spore assemblages of Richardson and Lister (1969). The stratigraphy and sedimentology of the area are currently being re-investigated by Professor J. R. L. Allen (Reading University) and Dr. B. P. J. Williams (Bristol University). The plant-bearing horizon described here is in their third grey sandstone/sandstone complex, which corresponds to Dixon's unit 8, his third 'green and grey band' (Dixon 1921, p. 41).

The plants are preserved as coalified compressions (*sensu* Schopf 1975). Streaks of iron oxide or, more rarely, iron sulphide are seen on some of the axes, but none are completely petrified. There are two broad categories of axis: narrow parallel-sided forms which, when they show dichotomous branching, are assignable to *Hostinella* Barrande, and wider less regular types often with coarse surface striations, probably of *Prototaxites* affinity. In both, a faint surface pattern is sometimes discernible under low magnification in ordinary light, but the same specimens observed using a stereoscan electron microscope or metallurgical incident light microscope show no cellular detail. The encrusting sheets of coalified material are less easily identified, being of animal (for example, eurypterid) as well as plant origin. When recovered on film pulls, the majority are found to be quite featureless, consisting of granular carbonaceous material, but some show the reticulate patterning characteristic of cuticles of *Nematothallus* Lang. These, together with the products of bulk maceration, will be described elsewhere. Film pulls were also taken from *Hostinella* axes and certain sporangia. The former were not particularly informative; cuticles were seldom seen although occasionally narrow strands, longitudinally aligned and possibly representing the remains of cell walls, were recovered. A few sporangia contained spores.

SYSTEMATIC PALAEONTOLOGY

Family RHYNIACEAE Kidston and Lang, 1920
Genus COOKSONIA Lang, 1937

Type species. Cooksonia pertonii.

Original diagnosis. Dichotomously branched, slender, leafless stems with terminal sporangia that are short and wide. Epidermis composed of elongated, thick-walled cells. Central vascular strand consisting of annular tracheids.

Background rationale. Although most of the terminal sporangia in the Freshwater East assemblage are readily assigned to the genus *Cooksonia*, these have presented considerable nomenclatural problems at the specific level. The simplicity of morphological organization of the fossils, together with their fragmentary nature and lack of anatomy, results in relatively few characteristics for use in a systematic analysis and may also result in the over-emphasis of minor morphological differences which themselves may not be real. It has been noticed, for example, that removal of a few grains of rock or organic material can radically alter apparent sporangium shape, while part and counterpart are occasionally not identical, because some organic material has been lost on splitting the rock. Thus, before specific diagnoses are presented, I propose to give a general description of all the *Cooksonia* sporangia present so that the range in sporangium form may be fully appreciated.

General description. All the specimens were photographed and then drawn and measured. In addition to sporangium width and height, the diameter of the axis at its junction with the sporangium was noted and, in the case of a tapering axis, its diameter when of constant width. Film pulls were then taken from the less well-preserved specimens. The data are presented in Table 1. Accuracy of measurement depended on the mode of preservation as well as on the shape of the sporangium and its subtending axis. There were no difficulties when the sporangium was clearly delimited being composed of a greater thickness of carbonaceous material than the subtending axis nor where, although very little organic material remains on the fossil, the rock area once covered by the sporangium was stained a different colour. Measurement of sporangium height and axis width was most difficult in the tapering specimens where the entire coalified compression had a uniform appearance or when little organic material remained.

As a result of this analysis it was decided to split the eighty-three most complete fertile specimens into two major groups based on sporangium shape. Thus in the following description, Group I contains sporangia in which height is roughly equal to width, and Group II has sporangia which are considerably wider than high. Each group has been further subdivided into three, using characters of the subtending axis. Representatives are drawn in text-fig. 1. It must be emphasized that these categories have been constructed purely for ease of handling numerous comparatively featureless fossils, and they should not at this stage be considered to have any taxonomic significance. Perhaps more relevant to the latter are a small number of intermediate morphology which do not fit exactly into any one of the six categories.

TABLE 1. Dimensions of fertile specimens assigned to the genus *Cooksonia* Lang.

| | Sporangium | | | | | |
| | Height (in mm) | | Width (in mm) | | Mean of sporangium height | No. of |
Category	Range	Mean	Range	Mean	sporangium width	specimens
Group I*a*	0·95–0·5	0·65	0·9 –0·4	0·66	0·99	10
Group I*b*	1·0 –0·28	0·49	0·96–0·3	0·51	0·98	22
Group I*c*	0·95–0·2*	0·58	0·85–0·4	0·57	1·01*	15
Group II*a*	1·3 –0·3	0·52	1·77–0·35	0·72	0·73	14
Group II*b*	0·55–0·3	0·45	0·73–0·4	0·62	0·74	8
Group II*c*	0·8 –0·27	0·47	1·7 –0·4	0·8	0·63	14

| | Axis diameter in mm | | | | $\dfrac{\text{Sporangium width}}{\text{Axis width}}$ | | |
| | Immediately below sporangium | | When parallel sided | | Axis immediately below sporangium | Axis when parallel sided | |
Category	Range	Mean	Range	Mean	Mean	Mean	No. of specimens
Group I*a*	0·38–0·1	0·17	–	–	4·08	4·08	10
Group I*b*	0·7 –0·15	0·27	–	–	1·98	–	22
Group I*c*	0·4 –0·15	0·28*	0·2 –0·07	0·14	2·26*	4·8	12
Group II*a*	0·5 –0·06	0·19	–	–	4·23	4·23	14
Group II*b*	0·4 –0·2	0·37	–	–	2·09	–	8
Group II*c*	0·9 –0·15	0·33*	0·45–0·1	0·15	2·8*	5·7	11

* Approximate measurements.

Group I, type a (text-fig. 1A). Each sporangium is more or less circular in outline (ratio of sporangium height to width ranges between 0·86 and 1·25) and is subtended by a parallel-sided axis whose width is small compared with that of the sporangium itself. The discrete shape of the two sporangia illustrated in Plate 2, figs. 1, 2, is typical but some (e.g. Pl. 2, fig. 4) have a less regular outline. Four specimens are branched (e.g. Pl. 2, fig. 9) the final dichotomy being some distance below the terminal sporangia. The subtending axes are either quite straight (Pl. 2, fig. 1) or gently flexuous.

The most important diagnostic feature of this category is the abrupt junction between parallel-sided axis and presumably spherical sporangium. There are, however, a small number of specimens (e.g. Pl. 2, fig. 3) where a very slight increase in axis diameter occurs *immediately* below the sporangium.

Group II, type a (text-fig. 1E). This parallels Group I*a* in axis characteristics but the sporangia are more or less oval (elliptical) in outline. Relatively few specimens are assignable to this category and these show considerable variation in morphology. For example, the symmetry of one of the largest sporangia in the assemblage (Pl. 2, fig. 8) may be compared with the irregular shape of that illustrated in Plate 2, fig. 7. The majority do not show branching, with just a short length of subtending axis preserved. NMW 77.6G.113 (Pl. 2, fig. 7) is a branching form with slender axes.

TEXT-FIG. 1. Line drawings of various shapes of *Cooksonia* sporangia. All specimens × 14. A. NMW 77.6G.105, B. NMW 77.6G.41, C. NMW 77.6G.23, D. NMW 77.6G.61, E. NMW 77.6G.13, F. NMW 77.6G.23, G. NMW 77.6G.6, H. NMW 77.6G.52, I. NMW 77.6G.113, J. NMW 77.6G.27, K. NMW 77.6G.33. A is assigned to *C. cambrensis* sp. nov. forma α; E to *C. cambrensis* forma β; B–D, F–H are assigned to *C. hemisphaerica*; I, K to cf. *C. caledonica* and J is left as *Cooksonia* sp.
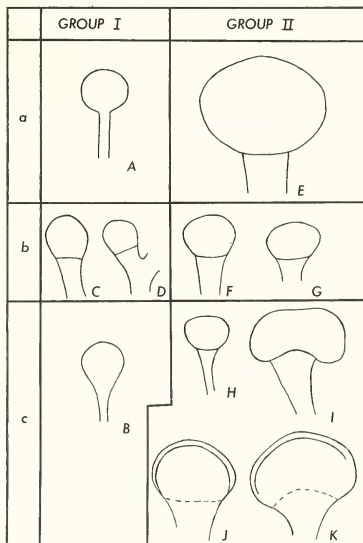
Branching is also seen in NMW 77.6G.21 (Pl. 2, fig. 10) where only the sporangia and distal axes appear to be completely preserved. Note that here the parallel-sided axes expand very slightly *immediately* below the sporangia and thus are similar to the specimens in Group I*a* illustrated in Plate 2, fig. 3.

Group I, type b (text-fig. 1C, D). Sporangia have circular outlines, but are sometimes flattened at the junction with the subtending axis. The ratio of sporangium height to width ranges between 0·83 and 1·18. The axis is wide at the point of attachment and then tapers very slightly below. The diameter of the subtending axis when parallel-sided is large when compared with sporangium width. The specimens are thus readily distinguished from those in Group I*a*. The sporangium itself is quite distinct, its carbonaceous residues being much denser than those of the axis (Pl. 3, fig. 2). Branching is common, the final dichotomy occasionally occurring immediately below the sporangia (Pl. 3, fig. 1) but more usually a short distance below (Pl. 3, figs. 2, 3, 6).

Group II, type b (text-fig. 1F, G). Apart from the difference in sporangium shape, my observations on Group I*b* are equally relevant here. These sporangia also appear to be very well preserved, having entire, regular margins. They are not much wider than the subtending axes so that, as in Group I*b*, the spore-containing regions are little more than swollen extensions of the stems (Pl. 3, figs. 4, 8, 9).

Group I, type c (text-fig. 1B). These may be distinguished from the specimens placed in Group I*b* by the increased tapering of the subtending axes, which become parallel-sided some distance below the sporangium junction. A typical example is illustrated in Plate 4, fig. 2. This is a case where it was impossible to measure sporangium height, unlike the specimen shown in Plate 4, fig. 4 where the sporangium is clearly delimited from the tapering stalk. On such specimens the width of the axis at the sporangium junction is found to be approximately the same as in Group I*b*. The majority of the axes are unbranched. Most of the measured sporangia are more or less isodiametric, but a specimen on NMW 77.6G.21 is extended vertically (Pl. 4, fig. 3) while narrower forms showing comparatively little increase in width are intermediate between Groups I*a* and I*c* (Pl. 4, fig. 6).
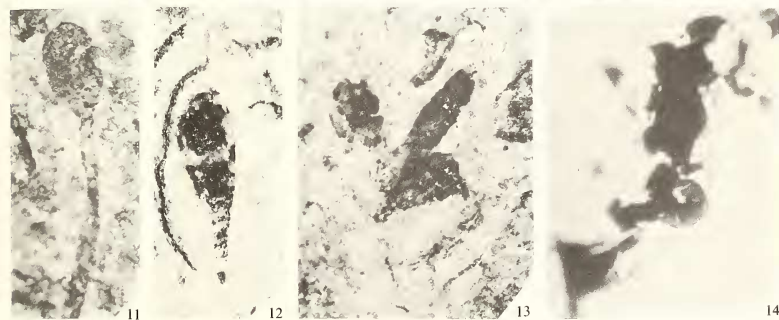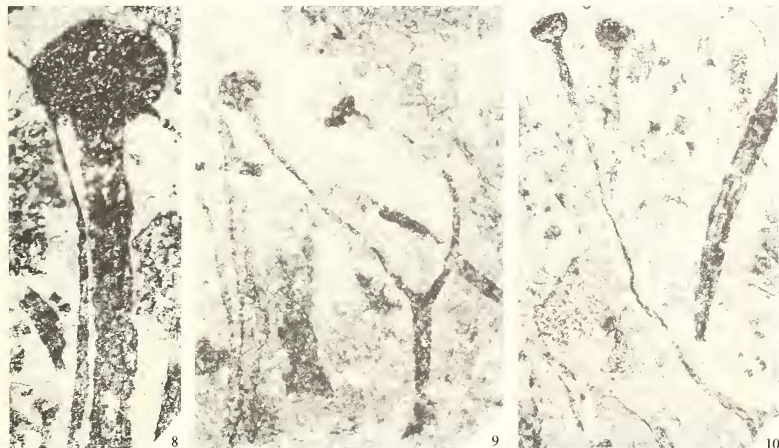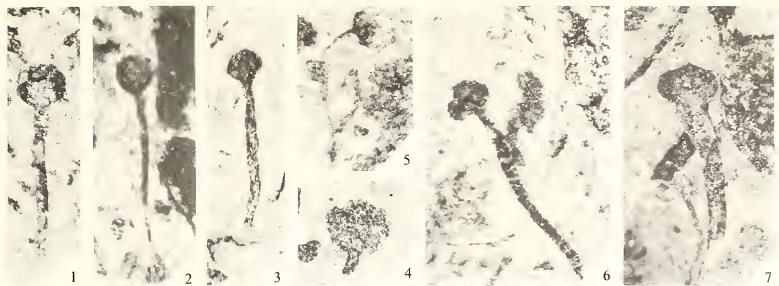
Group II, type c (text-fig. 1H–K). This is the category which shows greatest variation in morphology and size. A very small number may be considered the equivalents of Group I*c*, i.e. oval sporangia with strongly tapering subtending axes with occasional branching. An example with a particularly well-defined sporangium is illustrated in Plate 4, fig. 8. Specimen NMW 77.6G.100a bears a sporangium with slightly irregular outline (Pl. 4, fig. 9), which is preserved as a highly coalfield compression, the interstices between the granular carbonaceous material being filled with an orange substance, possibly limonite, the whole presenting a reticulate appearance. Some of this material was scraped off and mounted on a slide. Oval to circular, often irregularly shaped, light brown crystals were observed, but not spores. Examples of such crystals are illustrated in Plate 3, fig. 13. In the specimens already described, the junction between sporangium and stalk is seen as a straight line. There is, however, a small number of oval sporangia in which the distal part of the stalk extends into the base of the sporangium cavity so that a convex line marks the junction (Pl. 4, figs. 10, 14, 15). The representative of this type illustrated in Plate 4, fig. 14 is an unusual branching specimen in that the sporangium is overtopped by the second branch of the ultimate dichotomy.

Finally there are a few oval sporangia with distinct borders. The example illustrated in Plate 4, figs. 16, 17 has a short comparatively wide stalk (?intermediate with Group I*c*), the junction with the sporangium being almost straight. The central,

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PLATE 2

presumably spore-containing, region of the sporangium consists of dense carbonaceous material which is surrounded distally by a narrow band of less dense material. This border becomes narrower near the junctions with the axis. A similar structure is seen partially surrounding a possible sporangium in Plate 4, fig. 18.

Spores. As film pulls result in the almost complete removal of the sporangium from the rock, they were usually taken from less well-preserved specimens. Small amounts of coalified material were removed from the more morphologically informative sporangia and oxidized in Schulze's solution. In three instances, chips of rock bearing sporangia were mounted on stubs, coated with gold and examined using a stereoscan electron microscope. The film-pull method was the only successful one, with spores recovered from six specimens. In all cases they are fragmentary and have smooth walls. The diameters of the more complete spores (i.e. those where half or more than half the spore is present), together with some information on sporangium type, is given in Table 2. Note that spore size in the globular (Group I) sporangia is more or less uniform (Pl. 3, figs. 10–12) but the spores from the single oval sporangium (Group II) are markedly larger (Pl. 3, figs. 14, 15).

TABLE 2. Spore dimensions from sporangia of *Cooksonia* type.

Specimen number	Category	Range in spore size (μm)	Mean (μm)	No. of spores measured	Plate 3, fig.
NMW 77.6G.72	I*b* (branching)	24·0–30·0	27·0	7	10, 12
NMW 77.6G.17	I*b* (branching)	22·5, 24	–	2	11
NMW 77.6G.111	I*c*	25·5–37·5	29·5	14	
NMW 77.6G.38	I	22·5, 22·5	–	2	
NMW 77.6G.112	I	28·5–34·5	30·6	5	
NMW 77.6G.53	II (not *c*)	46·5–54·0	50·4	5	14, 15

Cooksonia hemisphaerica Lang

Plate 3, figs. 1–12, Plate 4, figs. 1–8; text-fig. 1, B–D, F–H.

Amplified diagnosis. Erect part of plant consists of dichotomously branching axes between 0·25 and 1·6 mm wide. Smooth axes terminate in sporangia of variable size and morphology including hemispherical, spherical, and elliptical forms. Sporangia are 0·3–2·0 mm wide and 0·2–2·0 mm high. Axes gradually increase in width below sporangia. Plant homosporous; spores smooth, circular, 22·5 μm–34·5 μm in diameter.

EXPLANATION OF PLATE 3

Figs. 1–3, 5–7. *Cooksonia hemisphaerica sensu* Lang 1937. All specimens × 15. 1, NMW 77.6G.17a. 2, NMW 77.6G.6a. 3, NMW 77.6G.23b. 5, NMW 77.6G.23a. 6, NMW 77.6G.1. 7, NMW 77.6G.94, unusually large, unbranched form.

Figs. 4, 8, 9. *C. hemisphaerica*: oval forms. 4, NMW 77.6G.6a, × 15. 8, NMW 77.6G.75b, × 15. 9, NMW 77.6G.27a, × 27.

Figs. 10–15. Film pulls from *Cooksonia* sporangia. 10, NMW 77.6G.72a; (F.P. (i)), fragmentary spores from isolated circular spore mass, × 320. 11, NMW 77.6G.17b (F.P. (i)), smooth spores from *C. hemisphaerica sensu* Lang, × 320. 12, NMW 77.6G.72a (F.P. (i)), fragmentary spores from *C. hemisphaerica sensu* Lang, × 288. 13, NMW 77.6G.109a (F.P. (i)), crystals of various sizes (arrowed) recovered from Group I type *Cooksonia* sporangium, × 640. 14, 15, NMW 77.6G.53 (F.P. (i)), larger smooth-walled spores from oval (Group II) *Cooksonia* sporangium, × 132.

PLATE 3

EDWARDS, *Cooksonia*
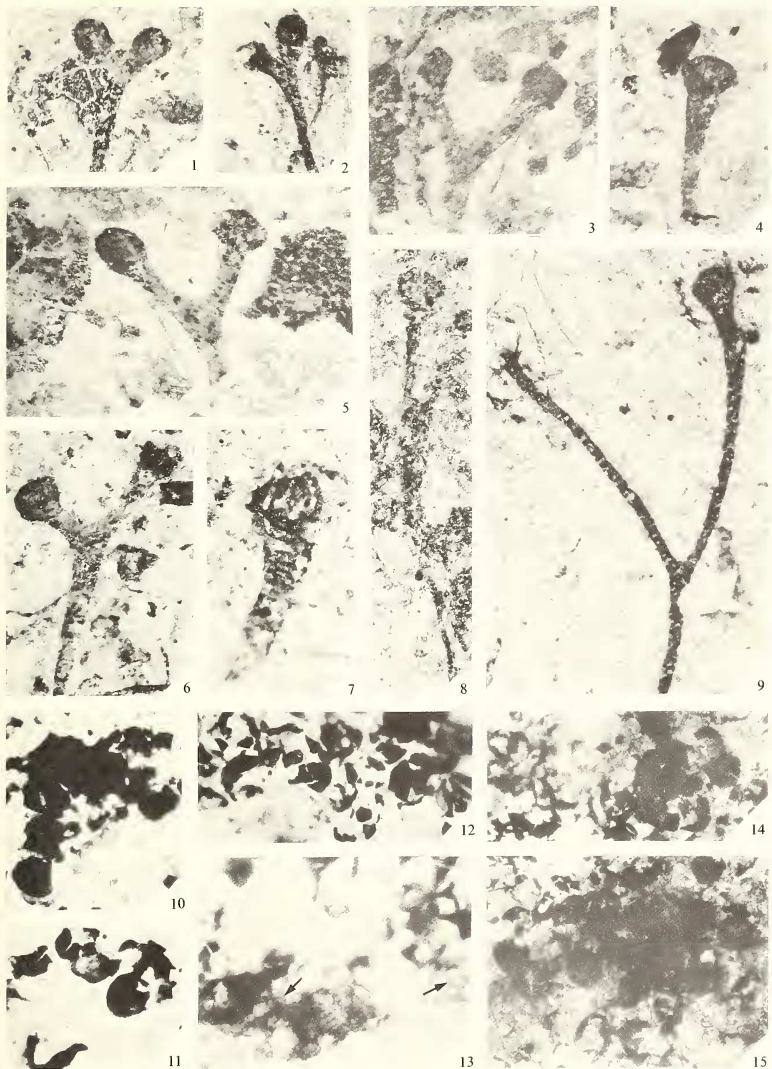
Holotype. V 58012 (Lang No. 181) illustrated in Lang 1937, pl. 9, figs. 31, 32.

Holotype locality. Quarry in Targrove beside drive to Targrove Hall.

Age. Downtonian.

Of the Freshwater East specimens described above, those in Groups I*b*, I*c*, II*b*, and a small number in Group II*c* will be included in *C. hemisphaerica*. Also included in the amplified species are the plants illustrated by Obrhel (1962, pl. 1, figs. 1-3, identified as cf. *C. hemisphaerica*) and certain of Ishchenko's specimens (e.g. those illustrated in Ishchenko 1975, pl. 14, figs. 1, 2, and 5). Excluded are the specimens described as *C. hemisphaerica* by Ananiev and Stepanov (1969).

Description and discussion. This was the only existing species of *Cooksonia* that it was immediately possible to recognize in the assemblage. The sporangia I have described in Group I*b* (Pl. 3, figs. 1, 2, 5–7) are directly assignable to *C. hemisphaerica*, which Lang erected for a small number of specimens from a single locality, a quarry in Targrove near the top of the Downtonian. He described the terminal sporangium as hemispherical, almost as high as wide, with thick walls and flat base. He illustrated three specimens (Lang 1937, pl. 9, figs. 31–36), all of which resemble the Freshwater East Group I*b* examples in over-all morphology although the sporangia of the latter are sometimes isodiametric or slightly taller than wide. The subtending axis in the Lang specimens is wide at the point of attachment and then tapers. Lang considered the sporangial width to be approximately three times the diameter of the axis, which he presumably measured some distance below the junction. This compares favourably with some of the Welsh specimens. All of Lang's examples are larger, the biggest sporangium being just under 2 mm high and just over 2 mm wide, while the smallest, which he considered immature, 1 mm wide and 0·96 mm high. Although he observed a central strand in one of his fertile specimens, this proved structureless. It is of great botanical interest that it was in sterile axes associated with these sporangia that he demonstrated tracheids with annular thickening, which he recognized as 'the most ancient piece of vascular tissue as yet demonstrated in position in a fossil plant in Britain' (p. 256).

Branching in the Freshwater specimens, like that in Lang's, is dichotomous. Neither he nor I have seen a pseudomonopodial branching system with dichotomously branching 'laterals' similar to that in Ananiev and Stepanov's reconstruction of *C. hemisphaerica* based on Lower Devonian specimens from Siberia (Ananiev and Stepanov 1969). I agree with Gensel (1976) that the Russian plants have much more in common with her *Renalia* than with the relatively simple dichotomizing Downtonian species, and perhaps should be excluded from the genus *Cooksonia*.

One of the most informative specimens in the assemblage is illustrated in Plate 3, fig. 5. It comprises a branching axis in which the left-hand fork terminates in a globular sporangium typical of *C. hemisphaerica*, but the right-hand one bears an elliptical sporangium of the type assigned to Group II*b*. (The illustration unfortunately gives the impression that the right-hand subtending axis is parallel sided, because some coalified residues have flaked off where it widens below the sporangium). Thus, assuming that both sporangia are completely preserved, this is a demonstration of intraspecific variation in sporangia of *C. hemisphaerica*. There is an alternative interpretation which I find less plausible. It is possible that each sporangium was ellipsoidal in life so that, depending on its orientation on burial, compression would result

in either a circular or an elliptical shape. I consider it more satisfactory to extend the diagnosis of *C. hemisphaerica* to include sporangia which are much wider than Lang originally described (i.e. oblate spheroids in life) as well as the more of less spherical forms. In both, the subtending axis is wide at the sporangium junction and tapers only a little below.

As already mentioned, specimens assigned to Group I*b* (now considered *C. hemisphaerica*) and Group I*c* differ only in the degree of tapering of the fertile axis and in the distance of the ultimate branching point from the sporangia, and some specimens may be of intermediate morphology (Pl. 4, fig. 3). Indeed it is possible to assemble a continuous series from sporangia with axes which taper to less than half the sporangial width, to those in which there is little change in axis diameter. Comparing only sporangial dimensions in Group I*b* and I*c*, there is little difference in the ranges of height and width (Table 1), although the means are slightly higher in Group I*c*. The diameter of the axis at the sporangium-stalk junction is more or less the same. I believe, therefore, that specimens assigned to Group I*c* should also be included in *C. hemisphaerica*. Some support for this comes from Lang's own specimens, which also show variation in axis size, although his figured examples are too few to allow satisfactory comparison.

My observation that sporangia of *C. hemisphaerica sensu stricto* Lang occur close to branching points while those of Group I*c* terminate narrower unbranched axes or are some distance away from a fork, leads to the further speculation that the difference may be a developmental one—i.e. that Group I*b* specimens are younger than Group I*c*.

Although *Cooksonia* with its smooth axis is not directly comparable to any extant pteridophyte, it seems likely that its mode of growth was similar, and that each naked aerial axis would have possessed an apical cell or group of initials, which at a branching point would have divided equally to produce two new meristems. The onset of reproductive activity (sporangia formation) would have resulted in the cessation of further growth of that particular axis. Thus, considering a fertile specimen such as NMW 77.6G.17 (Pl. 2, fig. 2), dichotomous branching would be followed by a short period of vegetative activity (involving cell division at the extreme apex and tissue differentiation and extension behind), after which the vegetative apex would be converted into sporangial initials and growth would cease. In NMW 77.6G.23 (Pl. 2, fig. 5) the period of vegetative activity would have been much longer, while in NMW 77.6G.6 (Pl. 3, fig. 1) sporangia were produced almost immediately after branching. On this model, sporangia in Group I*c* would develop after a considerable period of vegetative activity. My hypothesis involves a slight modification of this determinate growth pattern in that I suggest that the first three examples described above are young fertile specimens preserved soon after sporangium determination, while sporangia on tapering narrower axes are mature ones, the thinner axes resulting from purely extension growth. In support of this speculation are my observations that sporangia in Group I*b* almost always appear entirely preserved, while those in Group I*c* tend to be larger on average and less regular in shape, perhaps indicating some disintegration at maturity. I have found only one completely fertile specimen (NMW 77.6G.1) which shows unequal development of the products of an ultimate branch (Pl. 3, fig. 6). Here the right-hand branch is considerably longer and thinner

than the other, possibly indicating that it had begun extension growth. It is, of course, equally possible that the meristem divided unequally and that the narrower right-hand branch subsequently grew more rapidly or for a longer time before determination of the sporangium caused growth to cease. The sporangia themselves are of different shape, the more globular right-hand one unfortunately being less completely preserved.

Such delayed extension growth is seen during the maturation of the strobilus axis in certain lycopods, although not in the sporangial stalks themselves. A far more striking demonstration is found in the sporophytes of hepatics, where the cells of the unbranched seta (sporangium stalk) are differentiated in the embryo and further growth is almost completely by cell elongation. I consider it unlikely that an entire *Cooksonia* sporophyte would develop in this way.

Although I have already included Groups I*b* and *c* and Group II*b* in *C. hemisphaerica*, I am reluctant to extend the specific concept still further to encompass the more heterogenous Group II*c*, except for a small number of intact oval sporangia with tapering axes with sporangium height/width ratio similar to that in Group II*b* (Pl. 4, fig. 8). I would also include the few specimens of similar size and morphology which have rather irregular distal margins and which are possibly older, empty sporangia.

The rather limited information from *in situ* spores lends some support to my conclusions, because spore diameter in sporangia assigned to Groups I*b* and *c* (i.e. *C. hemisphaerica*) plus two undetermined globular sporangia is more or less the same (Pl. 3, figs. 10–12); the undetermined, irregular Group II sporangium which I would not include in *C. hemisphaerica* on morphological grounds, has markedly larger spores (Pl. 3, figs. 14–15).

I feel less confident in assessing the extent of intraspecific variation in the remaining specimens, yet I am reluctant to erect numerous species based on very limited numbers

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EXPLANATION OF PLATE 4

Figs. 1–7. Tapering, globular forms of *Cooksonia hemisphaerica*, all ×15. 1, NMW 77.6G.41. 2, NMW 77.6G.36. 3, NMW 77.6G.37a. 4, NMW 77.6G.42, intermediate form with *C. hemisphaerica sensu* Lang, 1937. 5, NMW 77.6G.68a. 6, NMW 77.6G.63, possible intermediate form with *C. cambrensis*. 7, NMW 77.6G.21.

Fig. 8. NMW 77.6G.52, *C. hemisphaerica* (oval form), ×15.

Fig. 9. NMW 77.6G.109, *Cooksonia* sp. with reticulate patterning, ×10.

Fig. 10. NMW 77.6G.3, ×15.

Fig. 11. NMW 77.6G.33, cf. *C. caledonica*, ×15.

Fig. 12. NMW 77.6G.10, cf. *C. pertonii*, ×15.

Fig. 13. NMW 77.6G.114, *C. pertonii* from type locality at Perton Lane, Hereford, ×3·8.

Fig. 14. NMW 77.6G.74, *Cooksonia* sp., ×15.

Fig. 15. NMW 77.6G.113, cf. *C. caledonica* (specimen subsequently destroyed), ×15.

Figs. 16, 17. NMW 77.6G.27a and b, *Cooksonia* with border, ×15.

Fig. 18. NMW 77.6G.35, ?sporangium with border, ×15.

Figs. 19–23. Axes with enations assigned to *Psilophytites* sp. 19, 20, NMW 77.6G.32a. 19, unbranched axis, ×10·2. 20, single spine from 19 enlarged, ×33·6. 21, NMW 77.6G.69a, unbranched axis with truncated spines, ×7·2. 22, NMW 77.6G.69b, single spine from counterpart of fig. 21, ×21·4. 23, NMW 77.6G.88, branching axis with crowded spines, ×7.

PLATE 4
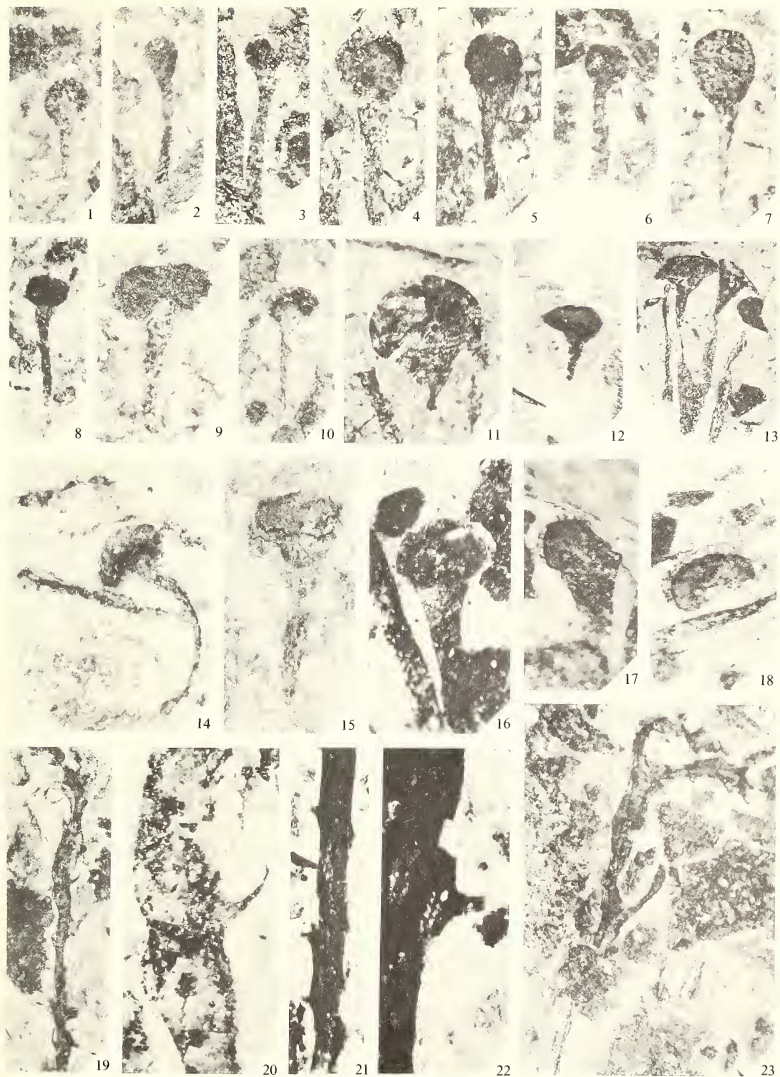
EDWARDS, *Cooksonia* and *Psilophytites*

of fossils, often of an exceedingly fragmentary nature. There are, however, a few sporangia sufficiently distinct to merit standard nomenclatural treatment (e.g. *C. cambrensis* sp. nov.). Others have some characteristics in common with, although not identical to, existing species (e.g. *C. pertonii*) while the remainder present new combinations of characters but occur in insufficient numbers to allow specific diagnosis.

Cooksonia cambrensis sp. nov.

Plate 2, figs. 1–10; text-fig. 1A, E.

Diagnosis. Aerial part of plant consisting of presumably erect, smooth axes 0·5–0·06 mm wide with occasional dichotomous branching. Terminal sporangia are circular to elliptical in outline, with subtending axes parallel-sided or increasing slightly in diameter immediately below the sporangium. Forma α includes sporangia circular in outline, 0·95–0·5 mm high and 0·9 to 0·4 mm wide. Forma β—sporangia ranging between elliptical, hemispherical, and irregular in outline, 1·3–0·3 mm high and 1·77 to 0·35 mm wide.

Holotypes. Forma α—NMW 77.6G.105 (Pl. 2, fig. 1). Forma β—NMW 77.6G.34 (Pl. 2, fig. 8).

Type locality. Foreshore on north side of Freshwater East Bay, near Pembroke, Dyfed. Nat. Grid. Ref. SS09 0236 9812.

Horizon. Lower Red Marl Group, early Downton (approx. equivalent to Pridoli).

Specific derivation. From Cambria (Wales). Forma α includes specimens described in Group Ia above. Forma β includes specimens described in Group IIa.

Description and discussion. This will include the specimens described in Group I where the sporangia are circular in outline and subtended by straight parallel-sided axes. The majority of specimens are unbranched but, where branching does occur (e.g. Pl. 2, fig. 9), it is some distance away from the sporangia. As I have no unequivocal evidence that the branched and unbranched specimens belong to the same plant, this is a case where it could be argued that the specimens showing no branching and in which vascular tissue has not been demonstrated should not be assigned to the genus *Cooksonia*. I believe that there are sufficient similarities in the characteristics of the sporangium and subtending axis to support the use of the genus. I have described similar organization in specimens in Group IIc, although here the sporangia have more or less elliptical outlines. The outstanding example is on specimen NMW 77.6G.34 (Pl. 2, fig. 8), notable for its large size, regular outline, and robust axis. The remaining specimens are less well preserved. Some have sporangia with flattened bases and hence hemispherical outlines. Again the majority are unbranched and, where branching is present, the axis is much narrower. I include these Group Ic specimens in the new species but, to distinguish the two major sporangium shapes, I designate the circular ones as forma α and the elliptical, forma β.

I also include those specimens where there is a slight increase in axis diameter *immediately* beneath the sporangium, as opposed to the gradual increase typical of *C. hemisphaerica*. An example of a globular form is illustrated in Plate 2, fig. 3, and an elliptical one in Plate 2, fig. 10. I have considered the possibility that these specimens are intermediate between *C. hemisphaerica* as defined above and *C. cambrensis*, which would in turn even further extend the specific concept of *C. hemisphaerica*. The important diagnostic feature here is the area of contact between sporangium and

subtending axis, which is more or less the same (and extensive) in all forms of C. hemisphaerica but small in C. cambrensis.

Affinities of the remaining Cooksonia sporangia

1. *Comparison with* C. pertonii. I have not found any sporangia which are immediately recognizable as *C. pertonii* Lang, although there is a very small number included in my Group IIc which show some similarity to the less typical examples in Lang's collection made from various localities throughout the Welsh Borderland. Little detail is visible on his plates, but an examination of his figured specimens housed at the British Museum and my own material collected from the type locality, Perton Lane, reveals that the majority of sporangia are considerably wider than high, resulting in a strongly flattened appearance (Pl. 4, fig. 13). The junction between sporangium and subtending axis is long and almost straight, so that the tip of the axis is nearly as wide as the sporangium itself, but it usually tapers rapidly (e.g. Lang's plate 8, fig. 7) although occasionally it remains more or less the same width (Lang's plate 8, fig. 12). The strongly flattened sporangia from Dyfed (e.g. NMW 77.6G.10 illustrated in Pl. 4, fig. 12) are much smaller than any of Lang's and so fragmentary that they are better left as cf. *C. pertonii*.

2. *Comparison with* C. caledonica. The sporangia in this Scottish Dittonian species are also variable in size and shape, but most are slightly wider than high. They too have tapering dichotomously branching axes which extend into the bases of the sporangia to varying degrees so that in extreme cases sporangium shape is reniform. The sporangia are further characterized by a narrow distal border (Edwards 1970).

There are no unequivocal representatives of *C. caledonica* at Freshwater East. A curved sporangium stalk junction is present in some Group IIc specimens (e.g. Pl. 4, figs. 10, 11, 14, 15). Of these NMW 77.6G.113 (Pl. 4, fig. 15), later sacrificed for spore preparations, is closest to the Scottish species and will be assigned to cf. *C. caledonica*. NMW 77.6G.3 (Pl. 4, fig. 10) will be left as *Cooksonia* sp. as will NMW 77.6G.74 (Pl. 4, fig. 14). The latter is unique in that although one of the daughter branches of the ultimate dichotomy terminates in a sporangium, the other is apparently sterile and considerably longer: an example of overtopping following dichotomous branching.

NMW 77.6G.33 (Pl. 4, fig. 11) has, in addition to a curved junction, a very narrow border represented by a strip of easily removed coalified material and will be called cf. *C. caledonica*. A much wider, less heavily coalified border is present on NMW 77.6G.27. On the counterpart, the sporangium stalk junction is slightly curved, but the over-all morphology of the specimen—an oval sporangium borne on a short stout axis—more closely resembles *C. hemisphaerica* (Group IIb) than *C. caledonica* (Pl. 4, figs. 16, 17).

It therefore seems likely that there was more than one kind of plant, in which sporangia had distinctive margins, in the Downtonian. This is also seen in the Lower Devonian, where sporangia with borders are not unusual, e.g. *Gosslingia* Heard, *Zosterophyllum* Penhallow, *Cooksonia crassiparietilis* Yurina and *Cooksonia* sp. (Croft and Lang 1942). In the first two genera, the rim is more heavily coalified than the central region and is believed to be involved in sporangial dehiscence (e.g.

Edwards 1969). A less dense rim, similar to those illustrated in Plate 4, figs. 16–18, has been recorded for undetermined *Cooksonia* specimens from the Brecon Beacons (Croft and Lang 1942) and here it is more likely that the border results from the compression of an almost spherical organ where there was a greater thickness of organic material in the central region, being composed of sporangial contents plus wall, than at the periphery where only the wall was compressed.

<div align="center">INCERTAE SEDIS</div>

<div align="center">Genus TORTILICAULIS gen. nov.</div>

Type species. Tortilicaulis transwalliensis sp. nov.

Diagnosis. Fragments of plants consisting of unbranched presumably upright axes terminating in elongate, fusiform to oval bodies interpreted as sporangia. Axes show occasional twisting especially immediately below sporangia.

<div align="center">*Tortilicaulis transwalliensis* sp. nov.</div>

<div align="center">Plate 5, figs. 1–12; text-fig. 2</div>

Diagnosis. Characters as in generic diagnosis. Axes 0·4–0·1 mm wide and at least 10 mm long. Terminal sporangia 3·9–1·1 mm high and 1·3–0·38 mm wide.

Holotype. NMW 77.6G.2 deposited at National Museum of Wales.

Holotype locality. Foreshore on north side of Freshwater East Bay, near Pembroke, Dyfed. Nat. Grid. Ref. SS09 0236 9812.

Horizon. Lower Red Marl Group, early Downton (approximately equal to Pridoli).

Derivation of name. Generic name *Tortilicaulis* is derived from the Latin adjective 'tortilis' meaning twisted and noun 'caulis' meaning stem. Specific epithet is from 'Transwallia' the Latin name for Pembroke (= across Wales).

Description. Elongate, fusiform to oval bodies attached to smooth stout axes are occasionally found. They are two to three times longer than wide and quite variable in shape. Although all attempts to isolate spores have failed, these elongate structures are assumed to be terminal sporangia. Branching has not yet been recorded in the subtending axes, which often appear to be twisted.

  Some indication of the variability in sporangium shape and size (particularly the length/width ratio) and in the morphology of the apex may be seen in text-fig. 2 and Plate 5. Of the long and comparatively narrow sporangia, some have typically attenuated tips and may be described as fusiform (text-fig. 2A, O and Pl. 5, fig. 7) while others are more bluntly rounded (text-fig. 2F, Pl. 5, fig. 12). This difference is paralleled in the wider sporangia which may be either ovate (text-fig. 2B, C, Pl. 5, fig. 2) or ellipsoidal (text-fig. 2L, Pl. 5, fig. 10) depending on the shape of the distal regions. Whether or not such distinctions are real is debatable, as the circumscription of the sporangium apex is often hampered by lack of organic material on the fossil and by staining of the rock (itself rich in disseminated carbon) in the immediate vicinity of the fossil. Table 3 shows that sporangia with rounded apices tend on average to be shorter than those with attenuated tips. Unfortunately the sample is too small for this to be of any significance. Indeed, evidence for a considerable size range in sporangia of

TABLE 3. Dimensions of most complete specimens of *Tortilicaulis transwalliensis* gen. et sp. nov.

| Sporangial shape | Sporangium | | Axis |
	Height in mm	Width in mm	Width in mm
A. *Fusiform*			
NMW 77.6G.7	2·3	0·67	0·1
NMW 77.6G.77	1·5	0·45	0·15→0·18
NMW 77.6G.2	3·9	0·95	0·4
Means for 3 specimens	2·57	0·69	0·22
B. *Fusiform with rounded tips*			
NMW 77.6G.7	1·7	0·5	0·1
NMW 77.6G.5a	1·3	0·38	0·1
NMW 77.6G.3	1·95	0·7	0·3
NMW 77.6G.47	1·5	0·55	0·1
Means for 4 specimens	1·6	0·53	0·15
C. *Oval with attenuated tips*			
NMW 77.6G.75a	3·5	1·3	0·2
NMW 77.6G.23b	2·4	1·0	0·3
NMW 77.6G.22a	1·9	0·8	0·1
NMW 77.6G.74	2·8+	1·1	0·3
NMW 77.6G.49	1·6	0·65	0·2
Means for 5 specimens	2·44	0·97	0·22
D. *Oval with rounded tips*			
NMW 77.6G.81	2·0	0·75	0·2
NMW 77.6G.5a	1·15	0·55	0·3
E. *Oval with mucronate tips*			
NMW 77.6G.37c	2·0	0·8	0·18
NMW 77.6G.1	1·45	0·6	0·20
NMW 77.6G.85	2·3	1·0	–
Means for 3 specimens	1·92	0·8	0·19
Over-all means (17 specimens)	2·07	0·80	0·20

identical shape is apparent in text-fig. 2H and N. Here the broad sporangia have distinctive, almost mucronate, tips (see also Pl. 5, figs. 6, 8, 9).

Accurate measurement of sporangial length was most difficult in the fusiform types where the sporangial bases taper gradually into the subtending axes. In the elliptical to ovate forms the junction is more obvious. Certain of the sporangia are slightly asymmetrical at the base, a condition often related to the twisting of the axis immediately below the sporangium (text-fig. 2H, Pl. 5, figs. 2, 8, 9, 11). In specimen NMW 77.6G.85 (Pl. 5, fig. 9) a definite constriction of the axis is visible in this region, but in others the axis is actually broken (text-fig. 2J, N and Pl. 5, fig. 7).

Subtending axes are of varying length, the longest being slightly more than a centimetre (Pl. 5, fig. 1). In contrast to what is seen in *Cooksonia*, branching has not been observed in these axes. Although they are more or less parallel-sided, they do not give an impression of stiffness or rigidity: indeed some are conspicuously curved. A distinctive feature is the twisting mentioned above. When present, this normally occurs

just below the sporangium, but some axes are further twisted proximally as in text-fig. 2B, Pl. 5, fig. 5. This specimen shows a definite constriction as opposed to folding, at each twist.

Very little has been discovered about the anatomy of the specimens. In the sporangia, carbonaceous residues either occur as flat sheets exhibiting clear fracture, or are granular. Spores were not seen on amyl acetate film pulls nor when small fragments were oxidized in Schulze's solution. Some specimens have the reticulate appearance
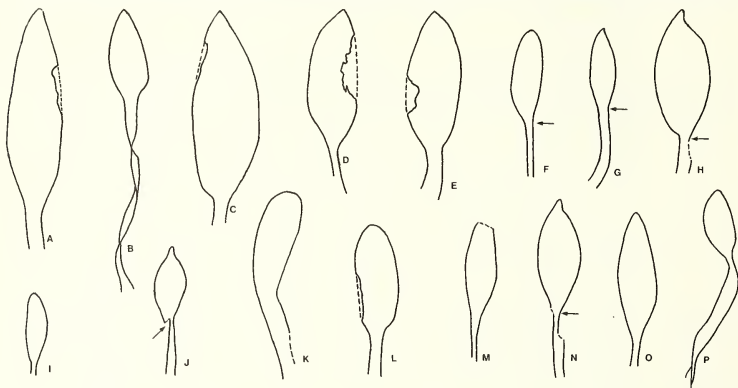

TEXT-FIG. 2. Line drawings of *Tortilicaulis transwalliensis* gen. et sp. nov. sporangia to show range in shape. All specimens × 10. Fusiform types: A. NMW 77.6G.2, G. NMW 77.6G.77, O. NMW 77.6G.13. Fusiform with rounded tips: F. NMW 77.6G.7, I. NMW 77.6G.5a, K. NMW 77.6G.3. Oval with attenuated tips: B. NMW 77.6G.49, C. NMW 77.6G.75a, D. NMW 77.6G.48, E. NMW 77.6G.23b. Oval with rounded tips: L. NMW 77.6G.81, P. NMW 77.6G.5a. Oval with mucronate tips: H. NMW 77.6G.85, J. NMW 77.6G.1, N. NMW 77.6G.37c. M is a specimen with tip missing. NMW 77.6G.44. Arrows indicate twisting immediately below sporangium.

EXPLANATION OF PLATE 5

Figs. 1–13. Sporangia of *Tortilicaulis transwalliensis* gen. et sp. nov. 1, NMW 77.6G.2, holotype, × 13·5. 2, NMW 77.6G.75a, · 15. 3, inset, NMW 77.6G.75a, specimen illustrated in fig. 2 after all organic material had been removed and photographed using unilateral illumination. Black line indicates approximate limits of sporangium, × 2·5. 4, NMW 77.6G.23b, robust sporangium with reticulate appearance, × 15. 5, NMW 77.6G.49, small sporangium with long unbranched twisted stalk, × 15. 6, NMW 77.6G.49, faintly striated sporangium with mucronate tip and constriction immediately below sporangium, × 15. 7, NMW 77.6G.7, fusiform sporangium, × 15. 8, NMW 77.6G.1, sporangium with oblique striations and break at sporangium/axis junction, × 23·25. 9, NMW 77.6G.85, sporangium with distinct mucronate tip, × 15. 10, NMW 77.6G.81, note reticulate pattern and asymmetric base, × 15. 11, NMW 77.6G.5a, small sporangium with broad twisting stalk, × 15. 12, NMW 77.6G.7, fusiform sporangium with rounded tip and twist immediately below, × 15. 13, NMW 77.6G.37a, isolated oval mass with reticulate pattern, · 12·4.

Figs. 14–18. *Pellia epiphylla*, an extant liverwort. 14, detached mature seta of sporophyte showing twisting, × 2. 15, part of mature seta with twisting, × 8. 16, cellular detail at twist, × 12·5. 17, capsule of sporophyte with twisted seta immediately below, × 12·5. 18, scanning micrograph of seta below capsule, × 22.

PLATE 5

EDWARDS, *Tortilicaulis* and *Pellia*
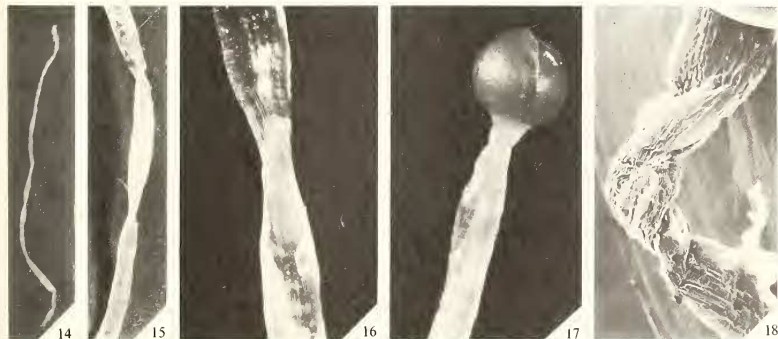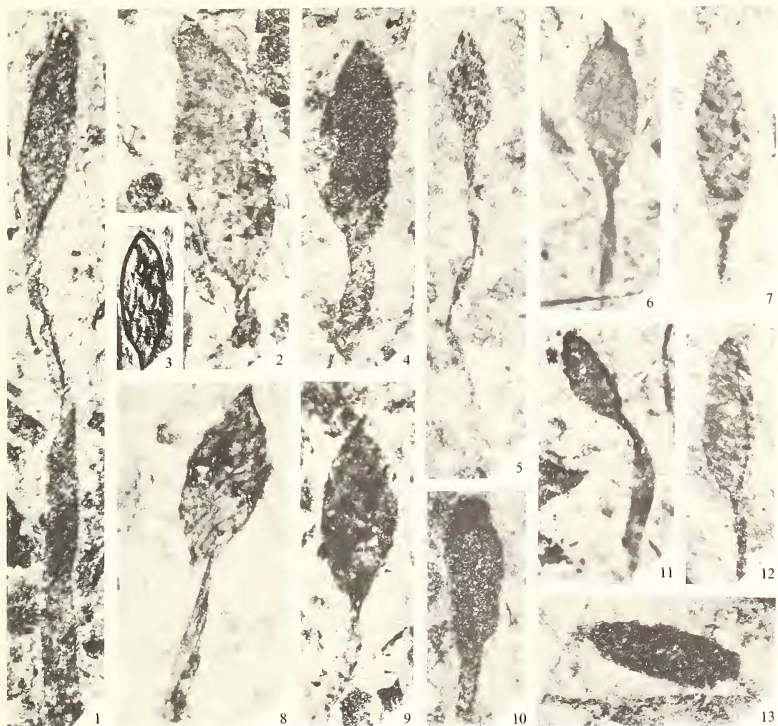
already described for certain *Cooksonia* sporangia (Pl. 5, figs. 4, 10). Here also, yellow-brown crystals together with some carbonaceous material were recovered from the film pulls. Also present in the matrix are discrete oval to fusiform bodies similar in size to the sporangia but lacking subtending axes (e.g. Pl. 5, fig. 12). These again failed to yield spores.

In a few cases, after most of the carbonaceous material had been removed from the sporangia on film pulls, obliquely running striations were visible on the rock beneath. This is most clearly seen in the specimen illustrated in Plate 5, fig. 7. Very fragmentary strands were recovered on the film pulls themselves. If these are the remains of cell walls, it would suggest that some of the cells of the sporangium wall were spirally orientated. Specimen NMW 77.6G.75 (Pl. 5, fig. 2), when viewed using unilateral illuminations, has a distinctly corrugated appearance, the interrupted ridges again being oblique. When all organic material was removed, it was noted that the rock itself shows a similar patterning (Pl. 5, fig. 3).

No structural detail is known for the axes and central strands have not been seen. It would be inadvisable on this evidence, however, to conclude that the plants were not vascular, as strands are only rarely present in the associated axes of *Cooksonia*.

Discussion. My investigations on this group are somewhat disappointing in that the critical information necessary for a comprehensive and conclusive discussion as to its affinities has not been discovered. For example, having failed to extract spores, I can only assume that the elongate bodies are sporangia. I should like to have found a much larger number of very long twisted axes before concluding that they are unbranched—absence of tracheids or even a central strand does not permit the conclusion that the plants were non-vascular, especially as I failed to demonstrate tracheids in the *Cooksonia* and *Hostinella* axes in the assemblage. Such limitations should be borne in mind throughout the following discussion.

Elongate sporangia terminating naked axes are characteristic of certain members of the Rhyniaceae (*sensu* Banks 1975). They include *Rhynia* Kidston and Lang; *Horneophyton* Barghoorn and Darrah; *Eogaspeseia* Daber; *Steganotheca* Edwards and Richardson and *Eorhynia* Ishchenko. Dichotomous branching has been recorded in all these genera, sometimes very close to the fertile region. Only the first three are known to have had vascular tissue. The apparent absence of branching in the Freshwater East specimens separates them from these rhyniophytes.

Long unbranched naked axes terminating in elongate sporangia typify the Lower Devonian genus *Sporogonites* Halle. The type species *S. exuberans* originally described from Röragen, Norway (Halle 1916, 1936) and since found in Belgium, Wales, and France, has large sporangia up to 9 mm long and 2 to 4 mm in diameter at the widest point. The smooth unbranched parallel-sided axes are approximately 0·5 mm wide and up to 10 cm long. In the original specimens, the sporangium apex is described as rounded, but the Belgian specimens (Stockmans 1940) have more pointed tips. The sporangium, of which only the upper half is considered spore-bearing, tapers gradually into the subtending axis. The surface of the sterile basal region has heavy longitudinal folding in some specimens, but this feature is lacking in more compressed fossils. Croft and Lang (1942) described stomata-like structures on the lower parts of semi-petrified Welsh sporangia. Two further species have since been

erected: *S. chapmanii* Lang and Cookson from Australia and *S. excellens* Frenguelli from Argentina. Halle tentatively suggested affinities with the psilophytes but this view was radically altered following Andrew's reconstruction based on Belgian material (Andrews 1960). Andrews described several fertile axes aligned in parallel which appeared to be attached to a carbonaceous film. He interpreted this as a bryophyte-like thallus to which several sporophytes were attached.

The Freshwater East specimens have much in common with *Sporogonites*. Although much smaller they are similar in shape, particularly when comparison is made with the Belgian *S. exuberans*, where the junction between sporangium and stalk is more distinct. Neither longitudinal folds nor sterile basal region are evident on the Welsh specimens, but this could result from preservation differences. The axes of *Sporogonites* are narrower (relative to sporangium width), longer, and straighter. It is interesting to note that one of Stockman's specimens refigured by Høeg (Høeg 1967, fig. 161A, p. 242) has a fold or twist some distance below the sporangium.

On the rather limited morphological data presented above, I conclude that these Downtonian sporangia have some affinity with *Sporogonites*, but as they do not show the well-defined characteristics of that genus, they should be placed in a new genus.

Systematic position of Tortilicaulis. As mentioned earlier, the possibility that *Tortilicaulis* was a vascular plant cannot be entirely eliminated. Should this have been the case it would be assignable to the Rhyniaceae in the Rhyniophytina Banks, 1975. Consideration of possible bryophyte affinities is prompted by its similarities with *Sporogonites*, in addition to the twisted nature of its axes. This latter feature is a characteristic of the mature setae (sporophyte stalks) of certain mosses and liverworts. Thus in *Pellia* the young sporophyte has a short stalk which elongates considerably due to rapid water uptake and at the same time twists (Pl. 5, figs. 14–18). The mature rather flaccid, twisted seta is hollow and when immersed in water (as would occur during the initial stages of fossilization) it does not straighten out. A compressed mature sporophyte of *Pellia* would thus look remarkably similar to *Tortilicaulis* except that the capsule in *Pellia* is spherical. The majority of capsules in the Jungermanniae are, however, ovoid to cylindrical, but modern forms are rarely indehiscent and there are no indications of a valvate construction in the fossils. Indeed the chances of such a delicate organ as a liverwort seta being fossilized must be very slim. Schuster (1966, p. 583) describes the seta of the Jungermanniae as 'an exceedingly ephemeral structure owing to the delicacy of its cells'. He points out that they have no intrinsic rigidity because all wall thickening is absent and there is no cuticle. The outermost cells of the mature hollow seta are obviously more robust than the remainder.

The seta of a moss is a much more resilient organ and some, for example *Discelium nudum*, are quite regularly twisted as a result of a spiral growth process. Herbarium material kindly donated by Dr. J. Duckett (Bangor) was immersed in water and the setae straightened out. Duckett considers this to occur only in young setae and that mature ones remain untwisted on rewetting.

Tortilicaulis thus has some features in common with bryophyte sporophytes, but there is little unequivocal evidence to support this grouping. I conclude therefore that the new genus should be left as *Incertae sedis*.

Family RHYNIACEAE Kidston and Lang, 1920

Incertae sedis

Description and discussion. A small number of terminal sporangia, although elliptical in shape, are longer than wide. They are not as large as *Tortilicaulis* specimens, both sporangium and axis diameters being similar to those in *Cooksonia*. A typical example is on NMW 77.6G.39 (Pl. 2, fig. 11). The subtending axis (4 mm long) widens at its base, perhaps indicating a branching point. In the remaining examples, axes are much shorter and unbranched. Considering sporangium shape, the specimens show some resemblance to the *Cooksonia* sp. described by Croft and Lang from the Lower Devonian of the Brecon Beacons and at present being revised in this laboratory. They are smaller and all except one lack the border already discussed for the younger specimens. The exception is an elongate sporangium 1·6 mm long and 0·7 mm wide which has a rounded apex and tapering base (Pl. 2, fig. 12). The central region originally consisted of a flat, smooth sheet of coalified material, which tended to flake off during the investigation, although some was removed and macerated. The border, a strip of coalified material, 0·1 to 0·12 mm wide, but narrowing slightly at the sporangium–axis junction adhered more closely to the rock surface. This sporangium is obviously quite different from any of the remaining terminal sporangia in the flora, but more specimens are required for an adequate circumscription of the new plant.

Finally, Plate 2, fig. 13 shows a small fertile specimen in which two sporangia are borne immediately above a dichotomy: that on the left is incomplete distally and 0·35 mm wide while the elongate sporangium on the right is at least 0·9 mm long and 0·3 mm wide. The axis before division is 0·2 mm wide. Smooth-walled spores recovered on film pulls are illustrated in Plate 2, fig. 14. This specimen is provisionally assigned to the form genus *Salopella* Edwards and Richardson, but until better material is found will not be given a specific name.

DESCRIPTION OF SMOOTH VEGETATIVE AXES

Hostinella sp. The most common sterile axes in the assemblage are smooth dichotomously branching stems assignable to the form genus *Hostinella* Barrande. They are parallel-sided and normally straight or very gently curved. Most specimens branch just once, the resulting axes being more or less equal in diameter, but very occasionally an unequal fork is seen (Pl. 6, fig. 4). Plate 6, fig. 5 shows a specimen in

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EXPLANATION OF PLATE 6

Figs. 1-13. Smooth sterile axes. 1, NMW 77.6G.22a, plant and animal fragments including typical *Hostinella*, ⨯ 10·5. 2, NMW 77.6G.108, block with narrower axes, ⨯ 17·5. 3, NMW 77.6G.89a, *Hostinella* with asymmetric branch pattern, ⨯ 7·5. 4, NMW 77.6G.18b, axis with unequal branching, ⨯ 6. 5, NMW 77.6G.3, *Hostinella* with double dichotomy, ⨯ 3. 6, NMW 77.6G.52, axis with short 'lateral' branches, ⨯ 8·5. 7, NMW 77.6G.19, wider axis with anomalous branching, ×7. 8, NMW 77.6G.40, axis showing some cellular structure, ×35. 9, 10, NMW 77.6G.37a and 37b, ×9, ×10·5. 11, NMW 77.6G.27, narrow axis with short lateral branch below dichotomy, ×4·5. 12, NMW 77.6G.52, cluster of branches, ×7. 13, NMW 77.6G.52, *Hostinella* with presumed vascular strands, ×9·35.
Figs. 14, 15. *Psilophytites* sp. NMW 77.6G.56a and 56b, ⨯ 10.

PLATE 6

EDWARDS, *Hostinella* and *Psilophytites*
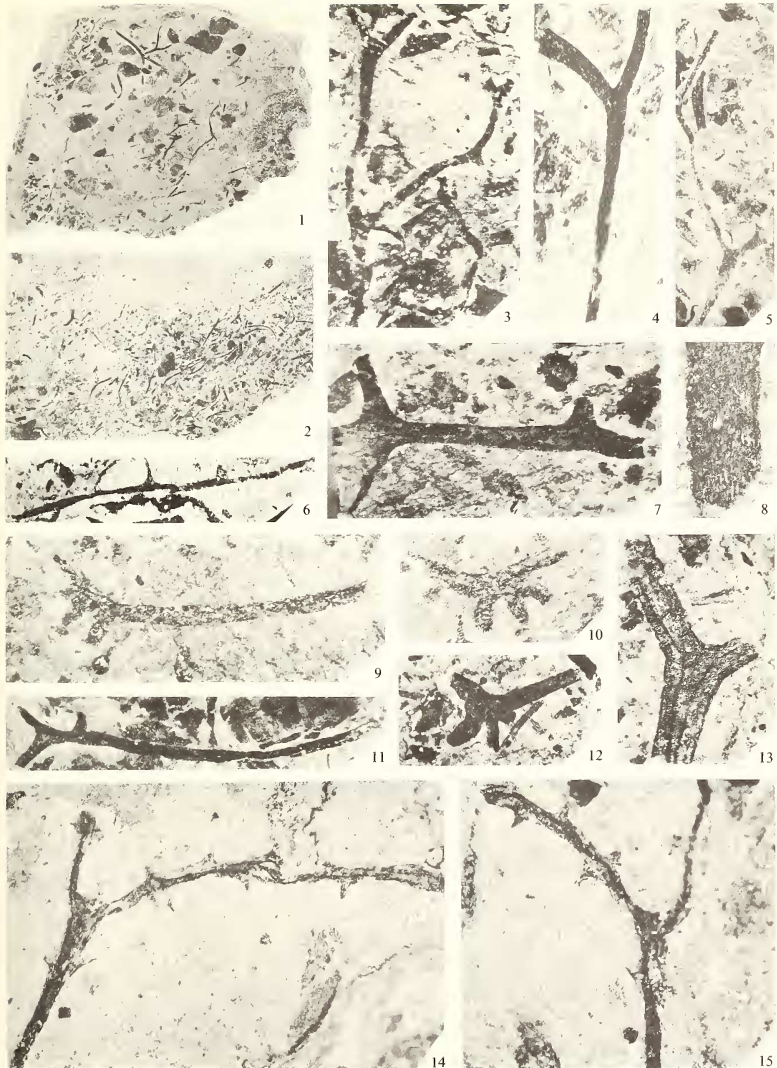
which more than one branch point is present and Plate 6, fig. 3 an example of a more profusely branching system with slight asymmetry in the branching pattern itself. The diameter of the axes varies between 0·05 mm and 2 mm (Pl. 6, fig. 1). Some blocks are covered by very narrow (0·05–0·1 mm) comparatively unbranched axes (Pl. 6, fig. 2). There is little change in diameter along a single specimen even in the more profusely branched types.

Little has been discovered about the anatomy of the axes. Cuticles have not yet been isolated from either bulk macerations or film pulls, although longitudinally aligned irregular strands of organic material, possibly the remains of cortical cell walls, have been seen on the latter. In the more heavily coalified specimens, longitudinal surface striations can sometimes be seen and also streaks of orange-yellow material, possibly limonite, perhaps replacing the cell contents (Pl. 6, fig. 8).

A few axes have central strands, which are normally narrow when compared with the total axis diameter and are thus characteristic of the rhyniophytes. Plate 6, fig. 3 shows such a strand having bifurcated some distance below the branch point. The occurrence of a much wider strand in two specimens suggests that perhaps more than one major group of vascular plants was present. Tracheids have not been seen.

Anomalous branching forms

(i) Specimen NMW 77.6G.52 (Pl. 6, fig. 6). This narrow featureless axis (maximum width is 0·15 mm) gives off three branches on one side and one on the other. Two of these lateral projections have wide bases and then taper. The curved longer one is 1 mm long.

(ii) Specimen NMW 77.6G.19 (Pl. 6, fig. 7). The complete specimen is 7·8 mm long and has a pair of opposite branches at one end and a single branch at the other. The main axis tapers from 0·6 mm to 0·5 mm in width. One of the pair of branches is sharply truncated, the other tapers. The solitary branch is rounded distally.

(iii) Specimens NMW 77.6G.27, 37, and 52 (Pl. 6, figs. 9–12). These three exhibit a concentration of branching at one end of a long otherwise unbranched axis. The orientation of these axes in life is unknown: thus they are all figured with the long axis horizontal.

Specimen NMW 77.6G.27 (Pl. 6, fig. 11) branches almost dichotomously at one end, but just below the branching point is a lateral projection slightly curved towards the branched end and ending abruptly. The entire specimen is 13 mm long and the main axis 0·5 mm wide. The main axis is striated and some of the cell contents have been replaced by limonite.

Specimen NMW 77.6G.37a (Pl. 6, figs. 9, 10). Here a slender axis, 0·4 mm wide and 5·3 mm long terminates in a cluster of four branches. The preservation of the axis is similar to that in NMW 77.6G.27. Although the ends of the axes appear rounded, they are actually broken off and end abruptly.

Specimen NMW 77.6G.52 is similar to the last one but has only three short branches the middle one having a rounded tip (Pl. 6, fig. 12).

Discussion. Branching in these three specimens is similar but not identical to the K-branching characteristic of *Zosterophyllum myretonianum* Penhallow, where it is normally confined to the basal region of the plant and is thought to contribute to its

tufted growth habit (Walton 1964). It is not unlikely, therefore, that these clusters of branches form the basal holdfast or are part of a more extensive rhizomatous system of a *Hostinella*-type plant. It must be emphasized, however, that they have never been found attached to dichotomizing axes nor has vascular tissue been seen. Thus the tuft of branches could equally well be part of the erect aerial system of a plant. In 1942 Høeg described *Hostinella* with axillary tubercles from the Downtonian of Spitsbergen. More recently I have shown that in the Lower Devonian *Gosslingia breconensis*, the tubercle may be a branch scar or represent the remains of the base of a branch (Edwards 1970), while Banks and Davis (1968) have described a short branch in the axillary tubercle position in *Crenaticaulis verruculosus*. Compression of such a specimen where overlying branches become fused together could produce a configuration similar to that in NMW 77.6G.27 and NMW 77.6G.52. Such branch patterns were not recorded by Høeg, although he did find small fragments of axes showing the characteristic branching of *Zosterophyllum*.

DESCRIPTION OF VEGETATIVE AXES WITH ENATIONS

Specimen NMW 77.6G.32a and b (Pl. 6, figs. 14, 15). One of the most exciting finds at this locality was a dichotomously branching axis bearing triangular enations, interpreted as spines, apparently arranged in two rows, one on either side of the axis. The over-all height of the specimen is 14 mm. The shorter branch, which is on the left in Plate 6, fig. 14 and has the best-preserved spines, is just over 4 mm long. The other which was uncovered extends for approximately one centimetre. It is possible that this was further branched, but the preservation is not good: little carbonaceous material remains and some pyrites is present. The axis below the branching point where spines are few is 0·5 mm wide. Measurement of axis width becomes more difficult distally because either the spines are crowded and have attenuated bases or the axis itself is poorly preserved. The axis is sometimes striated but no central strand is present. The spines appear to be attached to the sides of the axes, but a superficial attachment for some cannot be ruled out. Their arrangement is random, some alternate, while others occur in opposite pairs. Their shape is variable. The more complex spines are triangular with length of base roughly equal to height (e.g. 0·4 mm high and 0·35 mm wide at base). Others are attenuated basally (e.g. 0·47 mm at base and 0·25 mm high) and some have attenuated apices. An example of this is seen just below the fork where the needle-like tip is directed forward. In a few the apex is missing and the tip sharply truncated. The average height of the more complete spines is 0·29 mm and basal width is 0·34 mm.

Specimen NMW 77.6G.69a and b (Pl. 4, figs. 21, 22). Fig. 21 shows the counterpart of this unbranched axis 11·5 mm long and approximately 1 mm wide. Its margins are irregular and the surface of this heavily coalified compression is longitudinally striated. Three prominent projections, slightly asymmetric at the base and sharply truncated distally (Pl. 4, fig. 21), are visible on one edge of the axis. The largest is 0·35 mm high. The other side has the remains of bases of projections only. A prominent depression occurs on the axis surface near one end, indicating that at least one projection was superficially attached. The axis is far more robust than that in the preceding specimen. The dimensions of the enations are similar but it is impossible

to decide whether the truncated types in this unbranched specimen were actually peg-like, as for example is seen in *Psilophyton princeps* s.s. (Hueber 1967), or more spine-like but with fractured tips.

Specimen NMW 77.6G.32a and b (Pl. 4, figs. 19, 20). This unbranched flexuous axis is 6·5 mm long and ranges between 0·2 and 0·3 mm in width. It bears numerous spines of varying shape. Some are falcate (Pl. 4, fig. 20), tapering from a relatively narrow base to an almost hair-like tip (typical example is 0·15 mm wide at base and 0·4 mm high), while others are more robust with wider bases (*c.* 0·3 mm) and are less curved distally or broken off. The bases of some of the spines are overlain by the axis.

Specimen NMW 77.6G.88 (Pl. 4, fig. 23). Triangular enations are numerous in the upper part of this twice branched specimen overlapping both each other and the axis itself. Some of the spine tips are directed forward. Axis width is approximately 0·5 mm.

Discussion. These very fragmentary axes have some evolutionary importance in that, as far as I am aware, they are the only pre-Devonian spinous plants morphologically similar to the later Devonian genera *Sawdonia* and *Psilophyton*. There are a number of plants covered with appendages which are claimed to be lycopods or psilopsids from older rocks. These include the Cambrian *Aldanophyton* Kryshtofovich, the Ordovician *Boiophyton* Obrhel and *Akdalophyton* Senkevich, and the Silurian *Saxonia* Roselt and *Lycopodolica* Ishchenko. None have been shown to be vascular. Indeed some possibly have animal rather than plant affinities. Their numerous needle- or hair-like emergences do not resemble the non-vascular enations of either *Sawdonia* or *Psilophyton*. Although I have not demonstrated vascular tissue in the Downtonian axes, which are considerably smaller than later spinous specimens, I am convinced that should they have been found in Lower Devonian rocks they would have been assigned to Høeg's form genus *Psilophytites* (Høeg 1952). He erected this for frag-mentary sterile axes with spreading undivided spines of psilophytalean affinity intend-ing it to have a similar usage to *Hostinella*. This was before the unravelling of the exceedingly complex taxonomic tangle involving Dawson's *Psilophyton* complex. (For a full account see Banks, Leclercq, and Hueber 1975). It is now accepted that in the Gaspé flora there are two distinct types of spiny plant, *P. princeps* (Trimero-phytina) and *Sawdonia ornata* (Zosterophyllophytina) (Hueber 1967; Hueber and Banks 1967). Thus as Høeg anticipated, the fragmentary sterile spinous stems described from numerous Lower Devonian localities may well belong to quite separate taxonomic groups (Banks 1975*d*) making the usage of a form genus such as Høeg's highly desirable. It is perhaps a little unfortunate that the name may be taken to imply relationship with the genus *Psilophyton* itself and furthermore that its meaning is the exact opposite of what it describes (Gk. psilo-=smooth). But nomen-clatural considerations and revisions are best centred on Devonian specimens and I propose provisionally to call these spinous Downtonian axes *Psilophytites* sp., appreciating that they probably belong to at least two taxa of possibly widely separate affinity.

ENVIRONMENT OF DEPOSITION

The stratigraphy and sedimentology of the area is currently being revised by Professor J. R. Allen and Dr. B. P. J. Williams. They consider that Dixon's Basement Beds were accumulated on coastal sandflats influenced by the sea (pers. comm.), calcretes and mudcracks providing evidence for both prolonged and short exposure. It is considered that the sandstones and conglomerates probably represent channels and sand banks, perhaps partly intertidal. There is therefore the possibility that the plants grew on a saltmarsh. The fact that, although fragmentary, the individual fossils are not badly damaged, suggests limited transport and supports this suggestion. However, it is also a possibility that the plants lived on river banks or on mudflats surrounding lakes and were washed into the coastal mudflats where they were fairly rapidly buried.

GENERAL DISCUSSION

The composition of Downtonian floras has been mentioned only briefly here, but is more adequately surveyed elsewhere (e.g. Banks 1975c). *Hostinella* and *Cooksonia* predominate in the majority with the Podolian, and to a lesser extent, the Dyfed floras, showing greater diversity. I have actually seen only the Welsh Borderland fossils described by Lang (1937). My observations on his two *Cooksonia* species have already been recorded. In general the most striking difference between Lang's and the Dyfed plants is one of size, both axes and sporangia being considerably smaller in the latter.

My investigation of the Dyfed Downtonian flora is part of a much larger project involving the collection and description of plant macrofossils from Eltonian (lowermost Ludlow Series) to Downtonian localities in South Wales, an area where the stratigraphy is particularly well documented. Preliminary results are summarized in Table 4. Apart from Freshwater East, our most productive Downtonian locality is Capel Horeb (Edwards 1970) where in addition to *Steganotheca*, *Cooksonia* has now been recorded (unpublished data). Tracheids have not yet been demonstrated in Eltonian—Bringewoodian Y-axes but it seems not unlikely that vascular plants first appeared in this region in middle Silurian times or even earlier. The first indication that such Y-axes had rhyniophyte affinities comes in the Whitcliffian (Edwards and Davies 1976) where they are found attached to *Cooksonia* and *Steganotheca* axes. The present account produces some evidence for diversification in the Downtonian. Whether or not a similar evolutionary pattern was repeated throughout the world is debatable. Records of possible lycopods in the Late Silurian of Podolia (Ishchenko 1975), of lycopods in questionably Silurian rocks of Libya (Klitzch et al. 1973) and the prospect of the revision of the age of the lower part of the *Baragwanathia* flora in Australia (Gray and Boucot 1977) all indicate that further critical reappraisal is necessary before any generalizations are made.

Høeg (1952, p. 213) in discussing nomenclatural problems relating to the identification of fragmentary axes in the Lower Devonian wrote: 'It may be maintained that if a plant fossil is so incomplete, it does not merit mention at all.' To a certain extent this may be held true for the very fragmentary fossils I have described in this Downtonian

TABLE 4. Late Silurian stratigraphy in South Wales and Bohemia, incorporating records of macroplant fossils and environmental interpretations in the South Wales area. (Stratigraphy based on Cocks *et al.* 1971.)

Series	Stages Britain	Bohemia	Macroplant remains in South Wales (excluding calcified forms)	Environmental interpretation in South Wales
Post-Ludlow pre-Gedinnian (Downton)		Přídolí $\epsilon\beta_2$? ?	*Cooksonia* species *Steganotheca striata* *Tortilicaulis* *transwalliensis* *Psilophytites* sp. ?*Zosterophyllum* Y-axes + tracheids	Terrestrial fluviatile Brackish—sub- and intertidal Marine
Ludlow	Whitcliffian	Kopanina $\epsilon\beta_1$	*Cooksonia* sp. *Steganotheca* sp. Y-axes + tracheids	Marine shallowing Marine inshore
	Bringewoodian		Y-axes	Marine inshore-shelf
	Leintwardinian		Y-axes	Marine inshore-shelf
	Eltonian		*Powysia bassettii* (Edwards 1977) *Inopinatella* Y-axes	Marine inshore-shelf

flora, but like Høeg I consider it is important to describe, document, and, where possible, to identify such plants for future reference. The age of the flora is also responsible for perhaps an over-zealous treatment of minor differences in sporangium morphology. Certainly such a rigorous approach would not be applied in describing, for example, a truss of sporangia from the Upper Devonian *Rhacophyton* Mourlon. It has resulted, however, in a demonstration of inter- and intra-specific variation in *Cooksonia*, while the whole assemblage indicates a diversity of land vegetation much greater than hitherto known in the uppermost Silurian of Britain.

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